

BACKEBERGIA MILITARIS (AUDOT) H. BRAVO HOLLIS

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INTRODUCTION

Backebergia militaris (H. Bravo ex Sánchez- Mejorada, 1973) has always been a difficult plant for which to find a taxonomical position. It is included in the tribe Pachycereeae Buxbaum, sub-tribe Pachycereinae Buxbaum. However, its morphology and life cycle are distinct from those of all the other taxa included. Furthermore, it has a character which is unique in the whole Cactaceae family, that is, it bears an inflorescence with genetically determinate growth, a deciduous one, which for this exclusive character deserves a specific term, that I define as “Tiponche” (pron. teep- ònche), from the vernacular name by which the species is known in its distribution area.

The present paper describes for the first time the deciduous character of the inflorescence, and how this adaptation influences the dynamics of the life cycle of *B. militaris*. Furthermore, its functional significance is investigated, and related to a probable, sophisticated mutual symbiosis between the plant and a lepidopteran of the Pyraloidea, of a yet undetermined species. This study is the result of bibliographic research and of observations carried out both in the wild, during a survey in March 1994 in a locality within the distribution area of *B. militaris*, and with the dissection of authorized ¹⁾ samples collected on the same occasion.

NOTES ON THE STUDIES CARRIED OUT ON BACKEBERGIA MILITARIS

The species was discovered some 150 years ago, but the encounters between *B. militaris* and scholars of Mexican flora can still be counted on your fingertips. The reason for this are the features of the wide distribution area of the species; one of the hottest and most inhospitable regions of Mexico, very scarcely inhabited, with barely any roads and practically no place to stay.

B. MILITARIS IN HABITAT

The species is known in habitat with the vernacular name “Gorro de Grenadero” (= grenadier’s helmet) (Förster, 1886), “Organo de Gorro” and “Tipónche” (pron. teepónche). The westernmost edge of the distribution area of *B. militaris* is Jalisco, in the only known location for that State: Jilotlán de los Dolores. The site is located in the valleys that open into the Balsas depression, below 600 m of altitude. Going downhill towards south-east, along the river Tepalcatepec several populations are found near Apatzигán de la Constitución, down to the surroundings of the artificial lake formed by the “El Infiernillo” dam, into which the Tepalcatepec flows. Continuing towards south-east you go up along

the Balsas river, entering the State of Guerrero, natural border with Michoacán. The species is reported also along this river, particularly near the town of Ciudad Altamirano and further to the north. The occurrence of *B. militaris* is discontinuous and broken into populations with a relatively limited extension. Among the reports in the literature, the one of Petatlán (Guerrero) quoted by Bravo-Hollis in *Las Cactaceas de México* (1978) and referred to Sánchez-Mejorada, has not been confirmed and is considered a mistake, since it is located near the coast, where the climatic conditions are quite different from those of the areas where the species is found. The available data indicate that the distribution area falls within the eco-orographic region known as “the Balsas depression”. The geological, climatic and vegetational characters make this place a sort of natural ‘island’, quite distinct from the rest of the country.

Geology

Mexico is crossed by a volcanic range (El Cinturón Volcánico Trans-Mexicano), formed by the tectonic activity of the Pacific fault. The distribution area of *B. militaris* is located along the southern limit of the range, at an altitude varying between 100 and 600 m a.s.l.

Pedology

The soil in the region consists of sedimentary deposits of effusive origin, that have filled the valleys of the Rivers Tepalcatepec and Balsas already since the upper Cretaceous. This soil is generally rocky, little or not at all evolved, with limited accumulation of fine particles among the rocks where the plants grow. Poor and bare, unable to sustain a significant vegetation cover, the soils are exposed to superficial erosion. Along the river Tepalcatepec karst phenomena are also common.

Climate

The Mexican climate is often very dry and hot, however these conditions persist in winter only along the southern coasts. The Balsas depression prolongs coastal climatic conditions inland: the temperature there is always very high. In the areas near the ‘Infiernillo’ dam, daily maximum temperatures never go below 26 °C, while the hottest days can easily reach and go over 46 °C! Absolute minimum winter temperatures are near 5 °C. Because of the orographic conformation, a valley opening onto a huge extension, winds blow constantly and with a certain strength from north-west to south-east, all year round. Seasonal hurricanes often occur (25-41 per annum). Annual rainfall is between 400 and 1200 mm, with consistent rainstorms, but evaporation due to heat and wind is above 2000 mm of water in a year, so there is high relative humidity (65-75%) and a high drought index [$\text{Lang Index} = P(\text{mm})/T(^{\circ}\text{C}) > 30$, corresponding to a semi-arid or semi-dry climate].

Vegetation

From the floristic point of view, *B. militaris* grows in the area known as the “Balsas depression Province” (see map 1). The vegetation in this area is connected to the one on the Pacific coast through a narrow fluvial valley forming an isthmus, and it is isolated from the inner territories of the federation by a series of ancient mountain ranges. These conditions have favored the occurrence of local endemisms, with at least three genera: *Backebergia* of the Cactaceae, *Haplocalymma* of the Asteraceae and *Pseudolopezia* of the Onagraceae (Rzedowski, 1994) and about 350 species belonging

to several families (Rodríguez J.C., 2001). The Province is dominated by the Burseraceae family, that here shows the largest diversification in the whole country, and whose number of species is even higher than that of the legumes, usually dominant in Mexico. Within the province, *B. militaris* is in association with the typical 'Tropical Deciduous wood', characterized by bushy and arboreal species, whose leaves fall off during the winter dry period, that lasts at least six months. The species is also associated with a not well defined form of 'Thorny Wood' with thorny bushy and arboreal species [among which Mezquite, *Prosopis laevigata* (Willd.) M. Johnston] (Rzedowski, 1994).

Associated flora

In the location near the 'Infiernillo' dam *B. militaris* prefers slightly sloping positions in open woods. The caduceous species are mainly Burseraceae and there are also other columnar cacti [*Pachycereus marginatus* (DC.) A. Berger & Buxb., *Stenocereus kerberi* (K. Schum.) A.C. Gibson & K.E. Horak, *S. standleyi* (J.G. Ortega) Buxb., and *Isolatocereus dumortieri* (Scheidweiler) Backeb.]. The species avoids the eroded cliffs where it is difficult to anchor, and where the vegetation is dominated by small sized cacti like *Pilosocereus purpusii* (Britton & Rose) Byles & G.D. Rowley e *Ferocactus lindsayi* H. Bravo. Among the rocks it is easy to find compact cushions of *Mammillaria benekei* Ehrenberg. In the same distribution area the literature also reports: *Stenocereus fricii* Sanchez-Mejorada, *S. quevedonis* (J.G. Ortega) H. Bravo, *Pereskopsis rotundifolia* (DC.) Britton & Rose (Bravo, 1991); *Pachycereus pecten-aboriginum* (Engelm.) Britton & Rose, and *Acanthocereus occidentalis* Britton & Rose (Chalet, 2003); *Pachycereus tepamo* S. Gama-López & S. Arias (Anaya, 2000); *Bursera fagaroides* var. *purpusii* (Brandege) McVaugh & Rzedowski, *Stenocereus chrysocarpus* Sanchez-Mejorada (McCarten, 1973).

Human impact

Agriculture is practiced in the region, and the activities have altered the vegetation cover, especially in those areas that can be irrigated. Wide zones of 'Tropical Deciduous wood' have been cleared to make room for drought tolerating plantations and for traditional live-stock breeding. Generally, because of the unhealthy climate, disturbance is limited to the valley beds and some areas of the plateau.

Conservation status

To date the species is considered in good health, since known populations are intact and well preserved throughout a very wide distribution area. Starting in the seventies and on repeated occasions, the population close to the 'Infiernillo' dam, in Michoacán, has been subject to frequent collection of the terminal portion of flowering branches, so the species has been listed in CITES Appendix I. The control of importation, together with the difficulty of collection, packaging and posting, and the short life of the inflorescence, have convinced illegal collectors to abandon such activity. There has recently been a request to pass the species from CITES Appendix I to Appendix II. My personal considerations on the issue are the following: 1. Notwithstanding the vast extension of the distribution area of the species as a whole, the populations are disjunct and relatively limited. 2. Some populations are particularly exposed to the risk of illegal collection, because they are located near easily accessible paved roads. 3. The locality is militarized, but control on poaching is limited or absent. 4. The species is not cultivated anywhere, either with or without CITES certification. 5. The market is ever more aggressive with regard to uncommon and illegally collected succulent plants. 6.

The species has caught the interest of multinational pharmaceutical firms, maybe because of some active compounds whose composition and function is not revealed to the public. It could therefore be a natural resource that should be preserved in the interest of its country of origin. On the basis of these considerations, and notwithstanding the fact that its conservation status is good, in my opinion *B. militaris* should not be moved from its current position in the list of CITES species, that is Appendix I.

PLANT USES

According to information casually picked up on location, the plant is known and perhaps used in traditional medicine as a not better identified remedy.

MORPHOLOGICAL NOTES

Stem

The stem of *B. militaris* has a diameter of 12-15 cm and has 9-11 ribs. It grows rapidly, over a meter per year, and each new growth is revealed by a constriction, caused by the alternation of growth and rest phases. The development 'in segments' is found in other columnar species and in many African succulent trees (*E. ammak*, *E. eritrea*, *E. pseudocactus*, etc. ...), for which it is therefore possible to estimate the annual growth rate and the age of each branch. The variation in diameter of the stem of young branches is also a sign of the amount of rain fallen during their growth. The larger and older specimens have many broken branches, and stems break most easily where there are constrictions. In the specimens that haven't yet reached the reproductive stage, the spines are light coloured and on average more dense, due to the smaller diameter of the stem, and there are no secondary branches; plants grow solitary until they are about three meters high. In adult and old plants the stem is enlarged at the base, since there is secondary growth that forms a showy foot, dark brown due to the abundant production of periderm. The stems bear areoles. These are small, with 2-4 central spines about 1 cm long, gray and strong, and about 10 thinner radial spines, of the same length, with scarce and little persistent basal wool. In cultivation a rudimentary leaf may be seen at the base of the areole, but it falls off early and doesn't reach one millimeter in length.

From stem to reproductive structure

At maturity the apical growth of the stem changes deeply; at this stage the areoles are transformed from protective, sterile organs to fertile organs with a reproductive function (flowering organs). This transformation involves both the spines and the basal wool of the areole; at the same time there is a sudden increase in density, so the branch must rapidly change its developmental scheme to make place for them. This increase goes from the 9-11 initial orthostichies (rows of areoles arranged on the ribs) to the over 60 final orthostichies of the inflorescence, organized in 16 contact parasitichies (see Fig. 9). The ribs initially break up into tubercles, that quickly flatten occupying all the available surface. Within 3-5 centimeters the stem is transformed into a cylindrical turion bearing sunken areoles, from now on designated as the 'tiponche rachis'. The modifications of the areoles occur both in the spines (the central ones getting thinner and elongated along with the radial ones, until they all become bristly, glassy, yellow and about 5 cm long), and in the basal wool, that becomes more

abundant and thick, with fibers about 2 cm long. The transition from sterile branch to inflorescence may be sudden and equilateral, or asymmetric, occurring first on one side of the stem.

Tiponche structure

Observing a section of the tiponche it is possible to recognize several concentric layers, proceeding inwards. Externally there is a mass of bristly golden yellow spines, shiny and prickly, impenetrable because they are densely entwined. Their arrangement, together with the light colour and glassy shine, determines an interesting phenomenon of light reflection: when the sun rests on the inflorescences they appear lighted up, as if from the inside. Perhaps because of photochemically induced oxidative reactions of the chemical compounds in the spines, the colour does not remain constant in time, but it gradually darkens. Year after year the golden colour turns to hues of orange, burnt red, dark brown and finally black. This phenomenon causes the appearance of darker and darker bands, 15-20 cm high, each representing one year's growth. By counting them it is possible to establish the age of the inflorescence. The darkening of the spines is not exclusive of the species, but in its case it is quite rapid. Even though it is difficult to interpret the function of this phenomenon²⁾, it can be observed that the pale yellow flowers appear only on the portion of the inflorescence that is at least one year old, where they contrast better with the spiny background. Beneath the thick net of spines there is the soft and compact woolly matrix, about 2 cm thick, so dense that it is difficult to pass. There the flower buds develop, well protected, since they remain covered for a long period. Beneath the wool there is the inflorescence rachis. The part nearest the apical bud is slightly green, because of the sunlight reaching through the spines and the wool, that at this point are not as dense as along the inflorescence. The epidermis is thin, but 2-3 cm below the apex it becomes covered by a corky, conspicuous periderm, surrounding the areoles to form a semirigid involucre. This kind of suberification may be noticed also in species with a pseudocephalium, like *Cephalocereus columna-trajani* (Zavala-Hurtado, 1998), and in *B. militaris* it is so consistent that it contributes to the mechanical support of the whole inflorescence.

Like the areoles of the stem, those of the tiponche have a rudimentary leaf, slightly longer (± 2 mm) and soon falling off. The character appears to be shared with *Cephalocereus columna-trajani* (Karw.) K.Schum. and *C. senilis* Pfeiffer (Arias S., pers. comm.). Beneath the epidermis there is no chlorenchyma. The cortex is conspicuous, thick about 1/3 of the rachis diameter and made of spongy water-storage parenchyma, soft to the touch. The cambium is barely evident, and it delimits the pith that occupies the remaining third of the rachis diameter. Since the vascular bundles are quite fine, it looks as if their fibers have a limited role in mechanical support. The tiponche grows 10-15 cm a year, until it is 5-7 years old. At this point a strange and peculiar phenomenon occurs: it stops growing, degenerates, dies and falls from the plant to the ground. Observations carried out in the wild on tiponches at their terminal stage, still on the plant or recently fallen to the ground (see Fig. 21), have shown that the most frequent cause for degeneration is soft rot; cases of branches broken off probably by the wind are not rare. The collection and careful observation of numerous inflorescences found at the base of the plants, carried out especially on recently fallen material, still in decomposition, has not shown the presence of any seeds.

Blooming and flowering

Flowering occurs in March and April, with the new vegetative season. The flowers appear, solitary and casually distributed, on the portion of inflorescence formed in the years preceding the new vegetative phase (therefore in the older part, where the rachis is already well suberized). In most cases the

flower tube crosses through the whole width of the external bristles, extending outwards for a few centimeters; just enough to complete anthesis, which is nocturnal and lasts until the first hours of the morning. Flowers are not produced all at the same time, but gradually, so that every day there is a certain number of open flowers, for a period of perhaps one or two months. Apart from nocturnal anthesis, the flowers have a shape that specializes them for attracting moths: they are rather small, produce a limited amount of pollen and the fruit has few seeds (10-20).

Pollination, fruit-setting and seed dispersal

It is inferred that pollination is indeed carried out (preferentially) by moths, as explained in the paragraph on symbioses. The small fruits ripen in less than a month, and their scalar maturation allows seed dispersal over a large interval of time, during the first period of the rainy season that begins in April. The fruit is a berry 2 cm wide and 3 cm long. The pulp is mainly made up of the net of long, succulent seminal funicles. The pericarp is coriaceous and not showy, with scaly leaves on its surface, bearing wool and many bristly spines at their axils. The remains of the dry flower adhere to the fruit and extend outwards from the inflorescence's bristles. The system of seed dispersal still needs to be studied. Possible candidates are birds, that could extract the fruit from the inflorescence by pulling on the dry flower remains emerging from the bristles; however, these are quite prickly and apparently give no place to hold on to. Another possible candidate is some kind of ant: in nature I have observed a species of these insects with the habit of building narrow mud tunnels along the stems of *Backebergia*, up to the inflorescence. Since the tiponche is deciduous, it seems obvious that seed self-dispersal by gravity may occur. However, the observation of the total absence of seeds in some inflorescences and the almost complete absence of young plants near the adult ones leads me to reject this hypothesis.

Symbioses

The tiponche attracts a tiny fauna that lives amidst its bristles, well protected from the dangers of climate and possible predators. The fauna is made up of a certain number of arthropods, among which ants, mites and pseudoscorpions. With the exclusion of ants, that are perhaps commensal on *Backebergia*, these organisms do not live in symbiosis with the plant. The ripening fruits and the tiponche rachis, instead, host a particular insect that I have studied in detail. After dissecting an inflorescence of *B. militaris*, I noticed the presence of a tunnel going through the rachis, starting from an areole with the remains of an old fruit, emptied and dried up before ripening. The walls of the tunnel were covered with suberized cicatrization tissue, continuing with the periderm surrounding the rachis. Right near the fruit residue, protected by the bristly spines, I found a cocoon with the recent remains of a chrysalis. The remains were very light, translucent and amber-red, while the cocoon was made of a delicate, silky web. By carefully removing all the bristles from the tiponche I found some ripening fruits. Some of them hosted a single larva of a lepidopteran, intent on feeding on immature seeds and their fleshy funicles. All the old tiponches found at the base of adult plants showed unmistakable signs of the tunnels made by the larva of this moth, so that its presence in *B. militaris* cannot be considered an accident. I believe that this hypothesis is further sustained by the fact that already Lemaire had found this insect, as results from his 1847 description of plants coming from Jalisco: "... et in nonnullis ovariis plane dissecatis larvas cujusdam insecti observavi". My observations lead me to suppose that the larvae of this predator are born from an egg laid in the flowers when the adult visits them for feeding on nectar. After the egg hatches, the insect spends its immature stage living on a maturing fruit. This phase probably lasts a year, during which the larva must migrate into the rachis of the inflorescence it is feeding on, digging a tunnel in which it remains

all summer, autumn and winter. This migration is necessary because of the small size of the fruit. During the new flowering season, the adult emerges from the tunnel and visits the flower to feed on nectar and deposit eggs within the calyx, at the same time pollinating the flower and completing its life cycle.

DISCUSSION

Production optimization in columnar cacti

In columnar cacti, the vertical exposure of epidermis and chlorenchyma cells, and the wool shading the vegetative apex, allow protection from excessive heat. In this way, there is minimum heat accumulation when the sun is at the zenith during the warmest period of the year, while sunlight is used at its best for photosynthesis when it is at the horizon (early in the morning and late in the afternoon). This adaptation on one hand reduces the risk of heat damage, but on the other causes an under-optimal photosynthetic yield (Gibson & Nobel, 1986). In the specific case of *B. militaris*, the production of a large, non photosynthetic tiponche causes a strong and sudden shift of productivity towards net carbon loss. The need to optimize the absorption of photosynthetically active radiation (PAR)³⁾ must be evaluated on the basis of the particular ecological conditions in which the plants of this species grow, within their distribution area. To this regard, it may be useful to consider the adaptation of another columnar cactus species living at similar latitude: *Cephalocereus columna-trajani*. This species forms a pseudo-cephalium, usually towards north-east, and the apex also bends in the same direction. When photosynthetic yield decreases because of the pseudo-cephalium, there is a compensation due to the inclination of the upper part of the stem to north-west, causing an increase in PAR absorption. This inclination allows a lower absorption of radiation during the summer solstice (reducing heat accumulation) and a greater absorption during the September equinox, the period when growth is most pronounced. The inclination of the stem and the exposure to the north of the pseudo-cephalium have important effects also on the reproduction of the species: flowering occurs during the dry season, so the flower blossoms need more protection from excessive transpiration and from the sun-rays during the day (anthesis is nocturnal). To conclude, in this species with huge stems easily blown down by the wind, deprived of secondary branches, the inclination of the stem is the only way to increase reproductive performance, without compromising the normal development of the plant (Zavala-Hurtado, 1998). *B. militaris* occurs over a wide area, sub-horizontally elongated between the latitudes 19° 11' north (Jilotlán de los Dolores) and 18° 19' north (Ciudad Altamirano), and thus including also the area of *C. columna-trajani*, extending briefly to the north. In both cases light conditions are practically identical as for the incidence of sunrays, while with regard to temperature the habitat of *B. militaris* has higher mean temperatures in all seasons. With respect to *C. columna-trajani*, *B. militaris* could have greater problems of heat accumulation in the vegetative organs exposed to the sunrays. This factor may be critical for the life of a plant, especially if air temperature is above 46 °C, as in the Balsas depression. From this point of view, the morphology of the tiponche appears to be a better adaptation against overheating than that of the pseudo-cephalium. This is even more so if you consider that the tiponche allows the protection of probably the most important part of the plant, that is the reproductive organs. In many columnar cacti, layers of at least 10 mm of wool around the apex allow the decrease in temperature of living tissues down to 10 °C below air temperature during the summer (Gibson & Nobel 1986, Nobel 2002). In this case, both the thickness (> 50 mm), and the density (100%) of the bristles and hairs of *Backebergia*, allow a more effective insulation than that occurring in most of the species of columnar cacti with woolly crowns. On the basis of this evaluation, one of the advantages coming from an inflorescence like that of *B. militaris* with respect to the pseudo-cephalium of *C. columna-trajani*,

appears to be the achievement of a better seed production, both for its adaptation to local eco- logical conditions and for the amount of fruits that can potentially ripen. However, it is also true that the tiponche has a decidedly higher cost for the plant.

How much does a tiponche cost in terms of energy?

As already mentioned, the vertical stem of columnar cacti on one hand reduces the risk of overheating, on the other reduces the photosynthetic yield to sub-opti- mal levels. Columnar cacti show morphological characters which have evolved in order to optimize the absorption of PAR; among these characters are the presence of ribs and their depth (having an effect on the ratio vol- ume/photosynthetic surface), the ability to form branches and the spatial organization of these branch- es (Gibson, 1986; Nobel 1988). In *B. militaris*, the main character influencing the developmental behaviour of the plant is the self-limita- tion of growth due to the fact that all vegetative apices turn into tiponches. The tiponche is an organ that weighs heavily on the productivity of the individual as a whole and that, in comparison with a pseudo-cephal- ium or a non-specialized branch, requires a greater investment of resources (direct costs in terms of water, nutrient and dry matter consumption, and indirect costs in terms of reduced productivity due to the absence of chlorenchyma). In the end, the result is a growth habit with life phases corresponding to distinct morphological stages, and a sympodial branching pat- tern, anomalous for the large modern cacti within the whole Cactaceae family.

LIFE CYCLE

The life cycle of *B. militaris* in the wild comprises an immature stage, a juvenile stage, a mature stage and a senescent stage. The immature stage starts with germination, and in this phase the plant has a single stem with a shape similar to that of any other columnar cactus. The spines are denser and paler than those of the adult plants and no flowers are formed. The juvenile stage begins when the plant is 18-20 years old, with a height of about 2.5-3 meters. The growth of the apical part slows down (stem constrictions are closer) and an inflorescence develops rapidly at the apex, starting perhaps laterally but in a few cen- timeters interesting the whole circumference (Fig. 11). This process immediately affects the productivity of the individual: the plant keeps on growing, immobiliz- ing large amounts of carbohydrates in the lignin and cel- lulose that form the spines and trichomes of the wool, but the new portion of the stem (the tiponche rachis) cannot photosynthesize, so the cost is all on the green part of the immature stem. The cost will become even higher with the production of flowers, fruits and seeds, so the plant has an urgent need to produce a certain number of new, green, photosynthetically very active branches. Therefore the plant produces new branches, at about mid-height of the main stem. From the morphological point of view, these branches differ from the juvenile stage for having sparser spines, and little or no wool. They appear to be more efficient for photosynthe- sis. In the spring of the following year, the inflorescence produces its first (lateral) flowers. After seed maturation and dispersal, in the summer, a new portion of tiponche forms, simultaneously with secondary branches, and growth lasts for all autumn and part of the winter. This process continues for a few years (five to seven) during which flower production continues along all the tiponche (even in the older portions); eventually the tiponche reaches its maximum possible size, while the lateral branches begin producing their own tiponches. Again, the plant must form branches, of third order, to sustain the new inflorescences. After five-seven years the first tiponche ends its 'term'. Its weight can no longer be supported by the slender rachis structure, lacking mechanical fibers. Weakened by frequent bacterial infections that destroy its flesh, it breaks and falls under the gusts of wind that blow across the region during the stormy summers. After a few years, also the

branch that carried the tiponche breaks at a constriction near its branching point, being by now physiologically weakened and affected by bacterial diseases inherited from the tiponche. Sometimes healthy branches break off in the process, and in this case they may root and generate a new plant. While the first tiponche degenerates, those that have just reached maturity begin to flower, starting a cycle that lasts for the whole juvenile and mature stages of the plant. From this moment on, the costs for the plant in terms of productivity will multiply each time a new tiponche is formed, following a logarithmic progression that is a function of the number of new branches that the plant must produce to sustain each new inflorescence. At this point it is useful to refer to a mathematical model of what occurs in nature, on the basis of which it will be possible to make some considerations. Let us suppose that:

- a second order branch produces a new tiponche in exactly five years
- a tiponche reaches its full size after exactly five years, after which it decays
- the cost in terms of resources necessary to sustain a tiponche requires the production of at least two new branches

Then, a specimen of *B. militaris* will form a set of branches whose number increases exponentially: Age N° of branches N° of inflorescences

Tableau a refaire 20 3 1 25 6 2 30 12 4 35 24 8 40 48 16 45 96 32 50 192 64

This model predicts rather closely what is observed in nature, in the sense that the larger specimens do not reach a hundred branches and that the number of active tiponches is close to a third of the branches present; at a certain point, though, other factors occur, modifying the trend. When a specimen of *B. militaris* reaches a certain size, the demand for resources due to new inflorescences becomes so high that it can no longer be satisfied by the production of new branches, because the physiological limit of plant productivity has been reached. In theory, at this point the stage of maturity begins, when the ratio between the number of new tiponches and new sterile branches tends to one. This stage, likely brief, marks the beginning of a physiological crisis that strongly limits the production of young branches. This is the start of the senescent stage: for a certain period it is possible that the plant manages to recover productivity by losing many inactive inflorescences, and sustaining the last inflorescences till the end of their cycle. The situation becomes worse because the photosynthetic parts of the stem are by now old and covered with periderm, so they are also unproductive biomass. One by one the last tiponches reach their end, leaving the old plant with a few gaunt, bent branches, some only woody skeletons, until the plant finally dies. The above mentioned dynamics follow rather precisely what has been observed in the field; however further studies are necessary to verify the details of the process. I would like to point out that in the end, in order to produce the tiponche, this species has had to substantially change the branching model common among the more evolved cacti, that is the monopodial one, and go towards a sympodial one. However, the case under consideration is quite distinct from the other few examples of sympodial branching in the Cactaceae (see Figs. 38,39), since its architecture has clearly the function of bringing the development of all the tiponches to the same height. For this reason branching in *B. militaris* may be defined as pseudo-sympodial.

A deciduous inflorescence. Why?

Interesting questions arise from the fact that the production of a true deciduous inflorescence has been so important as to substantially modify the growth model and the life cycle of this plant. Why has a highly productive structure been perfected, if the life cycle that this determines heavily limits the longevity of individuals? And most of all, why is this the only case in the whole Cactaceae family, where convergent evolution occurs at all levels? It is true that the tiponche allows optimal flower, and therefore seed, production in harsh conditions, but it is also true that *B. militaris* lives beside many other columnar cactus species that seem not to need such adaptation, and successfully complete

their life cycle.

PARASITIC SYMBIOSES

Carrying out observations in the field and on sectioned tiponche samples, at first I undervalued a factor that has become quite important for this publication. In the wild, plants of *B. militaris* seem particularly susceptible to a bacterial infection that causes soft rot. The queer thing is that this infection occurs usually in well developed tiponches, close to their final size; I have observed that only later, after the tiponche itself has fallen to the ground, does the infection spread to the rest of the branch, which then decays (see Fig. 21). I believe that this problem is to be related to the larvae that usually infest the tiponche, similarly to what occurs in *Carnegiea gigantea* (Engelm.) Britton & Rose (Saguaro), another species of the *Pachycereinae*, that has a similar problem. In the latter case the infecting bacterium is *Erwinia carnegiana*, and the specific vector causing its diffusion within the cactus stems is supposed to be the larva of a moth (*Cactobrosis fernaldialis* Lepidoptera Pyraloidea). The larvae start feeding on the seeds in the ripening fruit, then they bore a hole in the epidermis and migrate to the stem, where they dig tunnels. Usually the Saguaro responds to their presence by forming a cicatrization callus that isolates the cavity dug by the caterpillar, but very often the hole in the epidermis allows the entrance of the spores of the pathogen, with a subsequent infection that may be fatal (Gibson R., 2002). After its death, the Saguaro leaves on the ground the remains of the tunnels formed by cicatrization calluses (see photo xx). In the case of the Saguaro, this kind of infection is very dangerous, being the first cause of death due to microbial pathology and affecting individuals of all ages. If the presence of *Cactobrosis fernaldialis* in Saguaro may be considered as a pure parasitic symbiosis, and the bacterial infection a casual consequence, the same might be said for the tiponche and the moth larva that infests it, which would be the cause of the subsequent infection. Indeed, the collection of detailed data on this phenomenon was aimed to give the most comprehensive picture of the ecology of *B. militaris*, contemplating also the presence of natural parasites.

MUTUAL SYMBIOSES

With the publication of Holland & Fleming's work (1999) on the symbiosis between *Pachycereus schottii* (Engelm.) D.R. Hunt (Senita) and the moth *Upiga virescens* Lepidoptera Pyraloidea (Senita moth), the role of the insect I had observed in *B. militaris* has acquired a completely different relevance. These authors conclude in their work that the relation between Senita and Senita moth is of a mutual kind, since there is a certain balance between the number of fruits consumed by the larvae and those reaching maturity, and that this cost is a good compromise for the plant, ensuring the timely presence of an ideal pollinator at flowering time. More recently, this phenomenon has been compared with other analogous cases of mutual symbiosis between plants and insects specialized for their pollination, which reproduce in the inflorescences (Dufaÿ, 2003). In all cases, the importance of plant control on insect larvae is clear, since they may be hosted only after completing pollination, otherwise the mutual symbiosis degenerates into simple parasitism. In the two known cases of 'perfect' mutual symbiosis, that is fig (*Ficus* ss.pp.) – wasp and *Yucca* (*Yucca baccata* Torrey) – moth, the insect's eggs are deposited in the flowers during pollination and the larvae develop at the expense of parts of the plant. In the case of the fig, the wasp larvae grow only in male flowers, and when the adult insects leave they are covered with pollen; these are the only ones able to come out of the inflorescence and transport it to the female flowers, that will be fecundated without allowing the deposition of eggs. In the case of *Yucca*, the moths reach maturity in

hermaphrodite flowers before anther maturation, so they flutter away and then pollinate and deposit eggs in the same flowers. In 70% of the cases, though, the larvae cannot grow at the expense of the seeds, because of the production of a barrier of sterile ovules, protecting the fertilized ones. In less evolved symbioses the control of larvae does not take place by suppressing them, but with other mechanisms limiting their development, as in other yucca species where the host plant regulates larvae survival by fruit abortion, if it carries too many larvae or too little pollen, or by regulating the number of seeds available for each larva. In the case of the symbiosis between the Senita cactus and the Senita moth, the larvae develop at the expense of seeds, ovules and even parts of the stem of the plant, with no apparent control mechanism. If proper parasitism does not occur in this case, it is due to the fact that immature populations of the moth are limited in their proliferation by other factors, such as drought, that provokes the abortion of many fecundated flowers and the death of eggs and young larvae, also predated by spiders (in the case of eggs) and wasps (parasites of the moth larvae) (Holland, 1999). For these reasons, this case of symbiosis is considered as a non mature step towards mutualism (Dufaÿ, 2003). Comparing the description of the symbiosis between Senita cactus and Senita moth with the observations on the sectioned tiponches from *Backebergia*, I have found some very interesting similarities (Table 3) From these similarities I infer that also *B. militaris* establishes a relation of mutual symbiosis with a lepidopteran of a yet undetermined species (see Table 4). A comparison of the characteristics of the symbioses between the two cacti and their respective insects leads to consider *B. militaris* and its moth as a more evolved model, while the relation between senita and its moth appears almost as a primitive form. In addition to those listed in the Table, there are two other characters that should be observed in more detail, that is the side-effects of the presence of larvae in the plant and the control mechanisms that affect the larval populations. As with the Saguaro, larvae that damage the epidermis of the host plant expose it to the entrance of dangerous bacterial spores. In the case of Senita, the larvae that can no longer feed on the ripening fruits move to the stem, that they eat while digging their tunnels. This exposes healthy and photosynthetically active tissues to destruction, even though the plants try to protect themselves more or less effectively from possible pathogens by forming cicatrization tissue (Holland, pers. comm.). Also in *B. militaris* the larvae, once they finish the available food in the fruit, move to the tiponche rachis, but this is a non-photosynthetic tissue, so the larva can feed itself and dig its tunnels without negatively affecting plant productivity. This is a condition similar to that of several *Chamaerops* species, where larvae of symbiotic weevils are hosted in the dry rachis of their inflorescences (cit. in Dufaÿ, 2003). And also *B. militaris* reacts to the presence of the larvae by forming cicatrization tissue. With an incidence that still needs to be verified, the presence of larvae results, sooner or later, in infective processes that lead to the destruction of the inflorescence, and on the long run to the loss of whole branches. According to above described life cycle, the early elimination of the tiponche stimulates the production of new inflorescences. Admittedly, the mutual symbiosis between the Senita cactus and its moth appears to have a weak point: it is not yet clear how the plant controls the development of the larvae growing at its expenses (as it is instead known in the case of yucca and fig). On the other hand, in the case of the symbiosis between *B. militaris* and its moth the control factor may be the programmed fall-off of the inflorescence. Referring to our mathematical model, according to which every five years a 30% loss of inflorescences occurs, and realistically assuming that within the populations of *B. militaris* the same number of individuals reaches this crucial point every year, it may be inferred that during each flowering season about 30% of the inflorescences are lost, together with their quota of larvae. This guess is based on the assumption that all the larvae are preferentially hosted within the inflorescence, as may be gathered by the presence of soft rot only in these organs, presumably due to the fact that the larvae damage the epidermis. Their presence only in this part of the plant could be due primarily to the concentration of flowers, the probable site of egg deposition by the moth, which should occur during pollination. Another reason could be the following series of factors favourable to larva and adult survival: • Better feeding conditions, because the fruits are the first source of food for the larvae; • Protection from high temperatures and dehydration due to the morphology of the inflorescence; • Maximum protection

against parasites and predators that cannot reach the entrance of the tunnels (for example, in the Senita cactus, endoparasitic wasps enter the tunnels and kill the larvae).

Control mechanisms of the larval populations

The control mechanism identified in this hypothetical mutual symbiosis could be self-regulated, in the sense that an increase in larval populations gives rise to an increase in soft rot, that would cause the premature loss of a larger number of inflorescences. Conversely, the decrease in the number of larvae would cause a longer life span of the tiponches, with an increase in flower production. An interesting and somewhat daring conjecture may be derived: the hypothetical mutual symbiosis could be not just limited to the interaction of two organisms (plant-insect), but it might involve a complex system, having on one side the host plant, and on the other an insect-infectious bacteria system including *Erwinia* sp., that becomes a third factor of fundamental importance. At this point it remains to be understood whether bacterial infections are regulated by endogenous or plant-insect symbiotic factors, or are totally dependent on external factors, carried by the insect. I do not exclude that this model could be extended to the mutual symbiosis ascertained in the case of the Senita cactus.

Factors of species-specific selection

Another object of further study should be the species-specific interaction between the two cacti *Pachycereus schottii*, *B. militaris* and their moths. This would further support the claim that these are analogous cases of symbiosis. To this regard we know that another moth, *Cactobrosis fernaldialis*, already mentioned in the case of the saguaro soft rot, deposits eggs on the Senita cactus flowers; however in this case the larvae feed on the fruits, but do not penetrate the stem, and they pupate elsewhere (Holland, 1999). Several studies have shown that the chlorenchyma of the stem of Senita and other cacti of the Sonoran Desert [*Pachycereus pringlei* Britton & Rose, *Carnegiea gigantea*, *Stenocereus thurberi* (Engelm.) Buxb., *Stenocereus gummosus* (Engelm.) A.C. Gibson & K.E. Horak] contains a high concentration of toxic alkaloids (in Senita, 15-20% of the dry weight). This has caused the selection of certain species of drosophila flies, each living in the rotting tissues of a single species, and not in others (Fogleman, 2001). Which leads to suppose that also the moth *Upiga virescens* has adapted in order to resist the lethal effects of the alkaloids, so it may feed on the Senita stem while digging the tunnels where it pupates, differently from what happens with the generic parasite *Cactobrosis*. Also *B. militaris* has a high alkaloid content; however, there are no studies reporting the alkaloid concentration in specific tissues, and it is not known whether the tiponche contains any. Therefore, it still remains to be investigated whether the presence of alkaloids can be related to the need of these plants to specifically select the species of symbiotic insect.

CONCLUSIONS

The above considerations lead me to conclude that *B. militaris* is a species that has evolved a specialized reproductive structure, due to the co-evolution with a possibly symbiotic lepidopteran insect. This structure may be defined as a deciduous inflorescence (with genetically determined growth), whose ontogenetic development relates it closely to the pseudocephalium of *Cephalocereus*. The morphology of this structure could optimize both plant reproduction and life cycles of the insect, whose larvae live at the expenses of the plant, feeding on a certain number of seeds and on portions

of the inflorescence. The inflorescence is deciduous, lasting on the plant for a period depending on the presence of the larvae, and this allows the symbiosis to be of a mutualistic kind, since by falling off it checks the larval population, avoiding a parasitic regime. Because of its originality, this reproductive structure deserves its own nomenclature, and I have called it "tiponche", from the vernacular name by which *B. militaris* is known in habitat. Within the tribe Pachycereinae, the tiponche is considered an apomorphic character, unique to this species, converging with the characters of the apical portion of the fertile branches of *Pachycereus schottii* (Senita). This structure too is to be considered as an adaptation to the mutual symbiosis with a moth species (*Upiga virescens*). In the Senita case, however, the adaptation leading to stem dimorphism is less specialized, and thus the fertile portion should be termed pseudo-tiponche. Even though the classification of *B. militaris* has a tormented history, I believe that its position within the genus *Pachycereus* (Hunt, 1987) should be questioned. The species has morphological characters, such as the deciduous inflorescence and the pseudo-symptodial architectural model, that are absolutely original within the whole Cactaceae family. Furthermore, the comparative studies based on DNA analysis within the group of closest species (Pachycereinae) shows well distinct traits, so that the resurrection of genus *Backebergia* may be proposed (Arias, 2003). FUTURE RESEARCH On the basis of the above considerations, it seems important to deepen the study of the reproductive ecology of *B. militaris*, its morphology and its life cycle. It would be particularly interesting to verify the occurrence of the above discussed symbiosis and to check whether it is truly mutualistic. To this end, it would be necessary to study the insect and the possible existence of species-specific selective mechanisms both in *B. militaris* and in the case of the symbiosis between *Pachycereus schottii* and the moth *Upiga virescens*. The definition of the actual conservation status of the species needs demographic and population studies, carried out also on a genetic basis, and extended to the whole distribution area.

Localities of *B. militaris*

Colima: Cited with no specific data (H. Bravo-Hollis, 1978) - not confirmed. Jalisco: Pico de Colima (Lemaire, 1847, perhaps today's Nevado de Colima), probably referred to the nearby location of Jilotlán de los Dolores (Chazaro, 1995 and Jean-Marc Chalet, pers. comm.) Michoacán: Type Locality: Basin of the Tepalcatepec river - near Apatzingán and, more to the south-east, the 'Infiernillo' dam (H. Bravo-Hollis, 1953). Pinzandaran, La Ceibita, Cinco de Mayo (Jean-Marc Chalet, 2003). Guerrero: Basin of the Balsas River - several locations (not specified, Anderson 1994), perhaps relative to Ciudad Altamirano (H. Bravo-Hollis, 1953); Petatlán (Sánchez-Mejorada cit. in H. Bravo-Hollis, 1978) - not confirmed, probably a mistake (it is outside the species' area of distribution)

Historique

The many changes in status and synonymy, and nomenclatural mistakes regarding *Backebergia* place it among the first positions in the Guinness of taxonomical rebuses.

1836/ *Pilocereus militaris* Hort. 1839 *militaris* = for the resemblance of the inflorescence to the helmet of English grenadiers, quoted in Förster, C. - Handbuch der Cacteenkunde, p. 652, (1886). Year of the discovery of the species, by the explorer Joseph Vandick from Antwerp, who collects some specimens and sends them to the collector M. de Jonghe in Brussels. The plants are observed by the French horticulturist M. Cels, who gives them their first name. 1845 *Cereus militaris* Audot - in *Revue Horticole* 2: 307 The French horticulturist Audot writes the first valid description of the species. 1845

Pilocereus niger Neumann - in *Revue Horticole* II, 2: 289 In the same publication the botanist Neumann describes a new cactus species seen at the Jardin des Plantes in Paris. They are samples donated by the Mexican politician and naturalist Melchor Ocampo, belonging to the same species discovered by Vandick. 1847 *Pilocereus chrysomallus* Lemaire, in *Flore des Serres et des Jardins de l'Europe* 3: 242 *chrysomallus* = with a yellow head M. Galeotti's herbarium is enriched with some cactus samples coming from the locality "Pico de Colima" (perhaps today's Nevado de Colima in Jalisco). Lemaire doesn't recognize the same species described by Audot and Neumann and writes a new description. 1849/ *Pilocereus militaris* Hort. ex Salm-Dyck, in *Cact. Hort. Dyck*. 1850 ed. II. 40. Invalid name 1880 *Cereus chrysomallus* (Lemaire) Hemsley, in *Biologia Centrali-Americani*, Botany 1: 541 Hemsley includes *Pilocereus chrysomallus* in the genus *Cereus*, creating a new combination of Lemaire's name. 1894 *Cephalocereus chrysomallus* (Lemaire) Schumann, in *Engler et Plantl, Pflanzenfam.* 3 (6°), 182 Schumann recombines *Pilocereus chrysomallus* as *Cephalocereus chrysomallus* and places *Pilocereus militaris* Hort., *Cereus chrysomallus* Hemsley and *Pilocereus chrysomallus* as syn-onyms. Pico de Colima becomes the type locality for the species. 1920 *Pachycereus chrysomallus* Britton & Rose non Lemaire, 1847, in *The Cactaceae*, Washington DC Britton & Rose reckon that *Pilocereus fulviceps* Weber (*Cereus fulviceps* sensu Berger) from Puebla (Tehuacán) is the same species described as *Pilocereus chrysomallus* by Lemaire and coming from Pico de Colima. When they create the new genus *Pachycereus* they include also *Pilocereus fulviceps* in it, but with the wrong name "chrysomallus" belonging to the plant described by Lemaire, and therefore they place in synonymy *Pilocereus chrysomallus* Lemaire, *Cereus chrysomallus* Hemsley, *Cephalocereus chrysomallus* Schumann, *Pilocereus fulviceps* Weber and *Cereus fulviceps* Berger. They include in the list also *Cereus militaris* Audot and *Pilocereus militaris* Schumann as probable synonyms. 1942 *Mitrocereus chrysomallus* Backeberg - in *Cact. J. DKG*, 48: 77 Curt Backeberg reckons that the formation of the cephalium, characteristic of the species from Tehuacán (*Pilocereus fulviceps* Weber), is a character sufficient to separate it from *Pachycereus*, and therefore he includes it in *Cephalocereus*, subgenus *Mitrocereus*, of which it becomes the type species. Also Backeberg's work is based on Britton & Rose's erroneous description; he doesn't bother to observe herbarium specimens and uses the epithet *Pilocereus chrysomallus*. At this date Backeberg raises subgenus *Mitrocereus* to the rank of genus and the type species becomes *Mitrocereus chrysomallus*: Britton & Rose's species from Tehuacán. 1953 *Backebergia chrysomallus* (Lemaire) H. Bravo, in *An. Inst. Biol. Mex.* 24:230 (1953) Helia Bravo-Hollis rediscovers the species after almost 106 years and decides to rename it on the basis of Lemaire's description of *Pilocereus chrysomallus*, clearing Britton & Rose's mistake and therefore creating a new monospecific genus. 1961 *Mitrocereus militaris* (Audot) H. Bravo ex Buxbaum, in *Bot. Stud.* 12: 54 Buxbaum declares that the species *Pilocereus chrysomallus* Lem., on which Bravo's description is based, is a *nomen confusum* and renames the species according to the rules of nomenclature, which impose the use of the last name considered valid. 1973 *Backebergia militaris* (Audot) H. Bravo ex Sánchez-Mejorada, in *Cact. & Succ. J. US* 155: 171 Sanchez-Mejorada points out that Buxbaum has wrongly referred to the name of a genus attributed to another species. However, he agrees with the need of abandoning the specific name *chrysomallus*. He adopts again the name *Backebergia* associating it with the specific name *militaris*. 1975 *Cephalocereus militaris* (Audot) H.E. Moore, in *Baileya* 19 (4): 166 Moore follows D. Hunt in widening the genus *Cephalocereus*, and includes in it *Backebergia militaris* together with *Mitrocereus fulviceps*. 1987 *Pachycereus militaris* (Audot) D. Hunt, in *Bradleya* 5: 93 David Hunt makes up for Britton & Rose's mistake, recognizing as valid the inclusion of the species in their genus *Pachycereus* and Audot's specific epithet. He does not offer any justification for such a revision.

WHERE DOES IT COME FROM?

Among the species closest to *B. militaris* there could be *Pachycereus pecten-aboriginum*. The young seedlings of the two species are quite similar (Fig. 13 *B. militaris*, Fig. 14 *P. pecten-aboriginum*): very large cotyledons, 7-8 ribs, numerous white acicular spines. Both *P. pecten-aboriginum* (on the left) and *B. militaris* (on the right) would have originated from an ancestor with spiny fruits (A). In *B. militaris*, the formation of the inflorescence occurred thanks to the co-evolution with a lepidopteran insect, through the stage of a pseudo-tiponche (B) (similarly to what can be seen today in the species *Pachycereus schottii* of Sonora), till it reached, due to the greater and greater concentration of fertile areoles at the apex of the stem (C), the stage of a true tiponche. The two evolutionary lines lead to opposite results in the number and size of fruits and in the concentration of flowers along the stem.

CEPHALIUM VS. PSEUDOCEPHALIUM VS. TIPONCHE

In many cacti there is evident dimorphism between sterile areoles, producing only spines, bristles and trichomes, and fertile areoles, that can also produce a flower bud. In many species of small globular cacti the fertile areoles completely substitute the sterile ones when the plant reaches reproductive maturity. They can be distinguished by their stronger and more conspicuous spines (*Coryphantha*) or for their spines transformed in bristles amidst abundant wool (*Discocactus*). In these cases, in a specimen reaching reproductive maturity all the areoles of the apical portion are different from those of the basal one, with little alterations in stem morphology. In other cases, the production of fertile areoles occurs only during a certain phase (flowering period) of plant growth, after which sterile areoles are produced again. In this instance there is a false cephalium, formed by these groups of fertile areoles, that may be lateral (*Cephalocleistocactus sensu Ritter*) or apical (*Arrojadoa*, *Stephanocereus*, *Neodawsonia*). In other cases still, dimorphism does not refer only to the areoles, but it also interests a portion of the stem, giving rise to evident morphological changes. Two different models may be distinguished: pseudo-cephalium and cephalium. The pseudo-cephalium has evolved independently in some genera belonging to the tribes Pachycereeae (*Cephalocereus*) and Cereeae (*Micranthocereus*, *Coleocephalocereus*). It is the group of fertile, densely pubescent areoles that develop preferentially along one side of the stem of columnar cacti. There the cortex is fully developed, and sometimes a thick periderm is produced, which stiffens the epidermis and therefore inhibits photosynthesis. When present, the periderm is produced after the stem has fully developed, and fuses together all fertile areoles. The cephalium has evolved independently in some genera belonging to the tribes Trichocereae (*Espostoa*, *Espostoopsis*, *Facheiroa*, *Trixanthocereus*) and Cereeae (*Melocactus*). It is the group of fertile, densely pubescent areoles that develop laterally on columnar species and on the apex of globular ones. It matures precociously (near the vegetative apex) and there the cortex soon stops thickening, so that growth is not congruous with the rest of the stem (Mauseth, 1999). In the case of columnar species the cephalium remains sunken in the stem, while in the case of *Melocactus*, where it is apical, its diameter is only a portion of that of the stem. In comparison with the two cases described, the inflorescence of *Backebergia* is morphologically similar to the cephalium of *Melocactus*. However, its ontogenetic characters bring it closer to a pseudo-cephalium. Indeed in this case too, the stem of the rachis can reach its maximum development in diameter, analogous to that of the stem, before the production of periderm (see the paragraph on tiponche structure). This analogy notwithstanding, the present study brings

evidence to absolutely original morphologic and functional factors (the phenomenon of 'programmed' detachment of the inflorescence, with all that this implies), that lead me to consider the inflorescence of *Backebergia* as a highly sophisticated structure, NOT homologous to cephalium nor to pseudo-cephalium. So original, indeed, as to deserve a distinct definition. For this reason I have chosen the term 'TIPONCHE' (pron. Teepònche), coming from the vernacular name with which the plants of *B. militaris* are commonly called in their distribution area.

B. MILITARIS IN CULTIVATION

After being rediscovered by Helia Bravo-Hollis, this plant has attracted collectors, but only at the beginning of the '70s did the collection and commerce of tiponche cuttings start. Probably, some expert collector of botanical rarities had noticed that a fallen off branch with inflorescence could root and grow normally. It is reported that in 1979, nurseries in Texas, close to the Mexican border, sold hundreds of cuttings with naked roots, or still to root. These plants were spread here and there throughout the world, but at costs too high for most of the common collectors, so that they became the attraction of the local merchant, who could show off his jealously kept and strictly not-for-sale specimen. After a while, those who had the 'luck' of buying these interesting plants soon found out that they were extremely difficult to keep alive: after producing a few flowers, the plants did not keep on forming the lovely inflorescence, but they became etiolated, or they grew new branches quite similar to those of any *cereus*. However, in most cases they stopped growing and the inflorescence died, leaving only, as a sad memory, a collapsed mass of blackened bristles. In view of what I have written above, it is easy to imagine that these cuttings could not live for long: the high request for organic matter caused an immediate crisis, and it was no use for them to elongate, trying to change a flowering branch into a photosynthetic one. The *Backebergia* plant with no tiponche, instead, grows without any particular problem. It can be treated as any columnar species from the 'hot' tropics, such as *Pilosocereus*, it enjoys adequate fertilization and grows rapidly. In order to flower, it needs a very tall greenhouse, where the temperature must be high all around the year (young plants can stand temperatures close to zero). The only known plant of this species who has reached reproductive maturity in cultivation is to be found in the botanical garden of La Habana, Cuba. Even though the climatic conditions in Cuba are fine, the specimen is kept in the greenhouse, probably to protect the cactus collection from too much rain. This has certainly determined the success in cultivation of this plant, known locally as the 'Russian Soldier', for its tiponche. This is an interesting example, because it allows the study of the life cycle of the plant in a location that is not subject to the local climatic conditions.

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1)

1 Permit number 09112 released by SEMARNAT the 9th of February 1994

2)

B. militaris is one of those species where darkening of an exposed wound occurs. This phenomenon has been related to the hydrolysis of a glucoside, lemainin, occurring in the presence of an enzyme or a strong acid like malate. The reaction gives a sugar (D-glucose) and an aglycon (3,4-dihydroxy-b-phenylethanol) that darkens rapidly when exposed to air (Gibson, 1986). If it were possible to demonstrate that the aglycon impregnates the bristles during their formation, the darkening of the spines could be traced back to the same phenomenon that brings about the darkening of the stem, occurring in a longer time due to the low permeability of the spines to oxygen.

3)

Of the whole range of electromagnetic radiation that make up the solar spectrum, only a portion is absorbed by photosynthetic pigments; this range, defined as Photosynthetically Active Radiation (PAR), is normally comprised between the wavelengths of 400 and 700 nanometers.

4)

CAN TE is the association that founded the botanical park "El Charco del Ingenio", open to visitors at San Miguel de Allende.

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